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SHORTER ARTICLES AND DISCUSSION

ŒNOTHERA NEO-LAMARCKIANA, HYBRID OF *O. FRANCISCANA* BARTLETT × *O. BIENNIS* LINNÆUS

Œnothera neo-Lamarckiana is a name which I propose for a synthetic hybrid that so closely resembles *O. Lamarckiana* De Vries that I do not believe systematic botanists could separate it from the latter by characters which would enter into a specific description. This does not mean that the hybrid is the exact counterpart of any particular line of *Lamarckiana* carried forward by the geneticists who are working with this form for it must be remembered that there are numerous biotypes of this species differing from one another in matters of greater or less detail, and that workers with œnotheras know that *Œnothera Lamarckiana* of systematic literature is a collective or polymorphic species, various forms of which can be isolated as biotypes in the experimental garden. In my studies of the *Lamarckiana*-like hybrids I am selecting towards the type known to us through the work of De Vries and through the seeds distributed by him.

The parents of my hybrids are *O. biennis* from the sand dunes of Holland and *O. franciscana* from California. I have given in a recent paper[1] the contrasting characters of these species together with descriptions of hybrids in the first and second generations. These parents were chosen after several years of search among the œnotheras for wild species that might be crossed with the hope of obtaining *Lamarckiana*-like types. In this connection my attention was first called to *franciscana* by Prof. Bartlett. In *biennis* and *franciscana* together are suggested all of the essential taxonomic characters of *Lamarckiana* and there seemed good reason to expect that among hybrids of the second and later generations would be found forms with combinations of characters approaching very closely to the peculiarities of *Lamarckiana*. In this respect my cultures now in the fourth generation have yielded results quite as satisfactory as I have hoped.

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[1] Davis, B. M., "Hybrids of *Œnothera biennis* and *Œnothera franciscana* in the First and Second Generations," *Genetics*, I, 197–251, 1916.

The results will, I think, show that *Lamarckiana*-like forms of *Œnothera* may be synthesized by simple crosses between wild species provided the parent species are selected with care. I believe that as the isolation of *Œnothera* types proceeds a number of different crosses will be found to give similar results, but this is the first successful combination that I have been able to study experimentally. My earlier work[2] with *Œnothera grandiflora* Solander and certain American wild types was planned at a time when *grandiflora* on historical grounds seemed to be a more important type in relation to the problem of the origin of *Œnothera Lamarckiana* than it does at present. That work was not so successful as the later in producing *Lamarckiana*-like hybrids for the reason that the parent species did not have as favorable characters for the end in view.

In spite of the recent paper of De Vries,[3] to which I have replied[4] in brief, my conviction is unshaken that Lamarck's plant, grown in the botanical gardens of Paris about 1796, was a form of *Œnothera grandiflora* Solander and can not be identified with the *Lamarckiana* of De Vries's cultures. On this view *Œnothera Lamarckiana* Seringe must pass into the synonymy of *Œnothera grandiflora* Solander. Neither am I convinced that other specimens in the collections of the Muséum d'Histoire Naturelle in Paris, particularly sheets of André Michaux and Abbé Pourret, may be referred to *Œnothera Lamarckiana.* I believe that the plant with which we are concerned in the experimental garden had a later origin and must bear the name of De Vries as its sponsor. At present our first certain date of the progenitors of *Œnothera Lamarckiana* De Vries appears to be about 1860, when the seed firm of Carter and Company in London introduced the plant to the trade.

Both De Vries and Gates have accepted my suggestion that Carter and Company obtained their material of *Lamarckiana* from some English station and not from Texas, as they state. We have no evidence that *Lamarckiana* ever grew in Texas and to me there is no evidence that it was ever native to America.

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[2] Davis, B. M., "Some Hybrids of *Œnothera biennis* and *O. grandiflora* that Resemble *O. Lamarckiana,*" Amer. Nat., XLV, 193–233, 1911. "Further Hybrids of *Œnothera biennis* and *O. grandiflora* that Resemble *O. Lamarckiana,*" *Ibid.,* XLVI, 377–427, 1912.

[3] De Vries, Hugo, "The Probable Origin of *Œnothera Lamarckiana* Ser.," *Bot. Gaz.,* LVII, 345–361, 1914.

[4] Davis, B. M., "Professor De Vries on the Probable Origin of *Œnothera Lamarckiana,*" Amer. Nat., XLIX, 59–64, 1915.

On the other hand, various races of *Lamarckiana* are at present growing wild in a number of English localities, the best known stations being on sand hills of Lancashire near Liverpool. A conspicuous *Œnothera* flora was present in this region as early as the beginning of the nineteenth century, as shown by an account in Smith's "English Botany," 1806. There seems to be no reason why *Œnothera Lamarckiana* might not have arisen in such a locality as a hybrid of species introduced into England possibly through Liverpool as a port of entry. Thus we are dealing with dates of introduction or origin that are reasonably close to present times; attempts to associate *Lamarckiana* with very early introductions into Europe appear no longer to have important support.

It is necessary to bear in mind this historical setting, since it may seem to my readers very improbable that *Œnothera Lamarckiana* should have arisen as a hybrid between *franciscana,* a species of western America, and *biennis* of Holland, England and other European countries. There is, however, nothing improbable in the possible meeting at Liverpool, with its world-wide commerce, of species of *Œnothera* from far corners of the earth. Furthermore, I should be the last to suggest that the particular races or species which give my *neo-Lamarckiana* have been the actual parents of the strains of *Lamarckiana* cultivated by De Vries. To strike the identical parental lines of such an assumed hybrid would in the case of the œnotheras be a most extraordinary piece of luck. It is remarkable that my results have proved so satisfactory; I have no doubt that other species crosses may sometime be made which will give hybrids as close or even closer to *Lamarckiana.*

The line of *neo-Lamarckiana,* which I now have in the F_4 generation from the original cross, was derived from a single selfed plant in the F_2 (14.53*c*), which fell well within the range of variation given by De Vries for *Œnothera Lamarckiana.* A description will later be published of this plant together with an account of its progeny through successive generations when these have been carried along somewhat further. The F_3 generation gave very few *neo-Lamarckiana* types, but these were closer to the large-flowered forms of De Vries's cultures. This F_3 generation was grown from earth-sown seeds and incomplete germination may have been responsible for the small proportions of *neo-Lamarckiana,* 7 in a total of 291 plants. The F_4 generation was grown this summer from what seemed to be the most promising plant of the F_3 (15.53*a*). This culture was from seed germinated in Petri dishes and was complete, since the residue of ungerminated seeds were empty of contents. From 764 seed-like structures 668 seedlings appeared, but there was at once a large mortality among weaklings most of which were unable to free their cotyledons from the seed coats. Only 558 seedlings lived to be potted and a further mortality reduced the number that was set out in the garden to 549. Of these plants 198 as rosettes presented characters of *Lamarckiana* while 351 developed rosettes for the most part with narrower leaves suggestive of *franciscana.* All of the shoots from the 198 *Lamarckiana*-like rosettes have shown *Lamarckiana* characters of foliage, inflorescence, and flowers but about one fourth of the plants seem likely to persist this summer as rosettes. The group of *neo-Lamarckiana* in the F_4 generation is therefore large constituting about 36 per cent. of the total number of plants in the culture.

In the group of *neo-Lamarckiana* there is some variation, but the best plants are so close to the *Lamarckiana* of De Vries that I can only distinguish them by small plus or minus expressions of a few characters. Thus the central shoot is not so strongly developed proportionally to the side branches. The leaves are a little broader. Sepal tips do not spread so widely. Buds may not be quite so stout. The pubescence is somewhat heavier over certain portions of the plants. Time will tell whether even these small differences can be eliminated by judicious selection through succeeding generations.

It is of course not enough for critical bearing on De Vries's interpretation of the behavior of *Lamarckiana* that a hybrid should be synthesized taxonomically similar to it. Such a hybrid must also show a behavior parallel to *Lamarckiana* in its essential features. The two striking peculiarities in the breeding habits of *Lamarckiana* are (1) its ability to produce two types (twin hybrids) in the F_1 when mated to certain other species, and (2) its peculiarity of throwing through successive generations the same types of "mutants" in small, fairly constant proportions. Late in the season of 1915 reciprocal crosses were made between *neo-Lamarckiana* (15.53*a*) and plants of *biennis* and *biennis* (Chicago), forms which De Vries has used in his studies on twin hybrids from *Lamarckiana.* The conditions were not favorable for the technique of crossing and I am repeating the experiments this year. However, I obtained from the cross *biennis* × *neo-Lamarckiana* two distinct classes of plants, (1) a narrow-leaved, smaller-flowered type with heavy pubescence and red papillæ (109 plants), and (2) broad-leaved forms, some larger-flowered, with a much lighter pubescence and few or no red papillæ (11 plants). Also, the cross *neo-Lamarckiana* × *biennis* (Chicago) gave two clearly defined classes distinguished at a glance by their size and foliage, (1) tall and narrow-leaved (64 plants), and (2) shorter and broad-leaved (11 plants). These crosses appear to have given twin hybrids and it should be said that the two groups were recognized and separated when the plants were in the rosette stage and that they consistently presented differences throughout all stages of their development. I shall from time to time make further studies of this behavior with different generations of *neo-Lamarckiana.* If *biennis* and *biennis* (Chicago) are pure species (a matter not yet established) this behavior would indicate that *neo-Lamarckiana* develops at least two classes of fertile gametes for both pollen and ovules. It thus seems probable that the behavior of *neo-Lamarckiana* when crossed to other species of *Œnothera* will parallel that of De Vries's *Lamarckiana* and thus support the view of several critics of the mutation theory that *Lamarckiana,* because it gives twin progeny in the F_1 of certain species crosses, must be itself a hybrid, producing different classes of gametes.

With respect to the ability of *neo-Lamarckiana* to throw "mutants" a most interesting situation is presented by its behavior this summer in the fourth generation. We have noted that a sowing of 764 seed-like structures gave 668 seedlings of which 198 developed as rosettes or mature plants into *neo-Lamarckiana.* Of the remaining 470 seedlings (668–198) only 351 lived to produce rosettes, a much larger group, however, than that containing the parent type, *neo-Lamarckiana.* We have then in the fourth generation *neo-Lamarckiana,* an impure or hybrid species, reproducing itself from at least 26 per cent. of its seeds. The exact percentage can not be told, for we do not know whether any plants of *neo-Lamarckiana* were among the 119 seedlings that died. In throwing a large progeny of a type very different from the parent F_3 plant, *neo-Lamarckiana* in the F_4 exhibited a behavior with strong resemblance to what Bartlett has described as "mass mutation." The types included a number of dwarf forms, but most of the plants resembled *franciscana,* although generally stronger, larger-leaved, and with considerable variation in flower size. It should be noted that no forms similar to the parent *biennis* were present; this type of segregate seemingly is either not produced or appears but rarely.

The conditions of sterility in *neo-Lamarckiana* are likely to bear directly on the peculiarities of its behavior in comparison with that of De Vries's plant. My hybrids agree with *Lamarckiana* in having pollen about one half sterile, but the F_3 parent plant of this year's cultures showed seeds 87 per cent. fertile while the seed fertility of *Lamarckiana* is much lower, being reported by De Vries in extensive experiments as from 34.5–46 per cent. and for two lines of mine running in tests 26–30 and 32–36 per cent., respectively. The variation noted by De Vries is believed by him to depend upon whether or not the plants are heavily manured. The question at once arises may not the mass variation of *neo-Lamarckiana* in the F_4 be correlated with its very much higher seed fertility? What would happen if *neo-Lamarckiana* should develop a greater degree of seed sterility or if some lines should be segregated with seed sterility approaching that of De Vries's *Lamarckiana?* Would the plants eliminated come from among the *neo-Lamarckianas* or would they come from the assemblage of variants from this parent type? Should they come from the variants, as seems to me probable since *neo-Lamarckiana* is a sturdy plant, then a condition might be reached where the variants would appear rarely or in small proportions and this would parallel exactly the present behavior of De Vries's *Lamarckiana* in throwing its "mutants." I shall watch intently for indications in my cultures of increased seed sterility and among my plants of *neo-Lamarckiana* select steadily towards the higher degree exhibited by *Lamarckiana.* It is interesting that the last stages in the experimental synthesis of a *Lamarckiana*-like hybrid should be concerned chiefly with selection towards a definite degree of seed sterility.

Œnothera neo-Lamarckiana illustrates clearly my concept of an impure species of *Œnothera.*[5] It is a plant that breeds true in a proportion of its offspring but is heterozygous since it develops varied types of gametes as proved by the assemblage of offspring which differ sharply from the parent plant, and further indicated by its behavior in producing twin hybrids. The facts of a high degree of pollen sterility (about 50 per cent.) together with a certain amount of seed sterility indicate the probability that other classes of gametes are eliminated or fail to function and that possibly certain types of zygotes may be formed which are unable to live. *Œnothera neo-Lamarckiana* therefore shows itself to be impure or heterozygous because it develops different types of gametes even though the plant when selfed reproduces itself in a fairly large proportion of its progeny. This behavior seems to me quite the same in principle as that of De Vries's *Lamarckiana,* the only difference being that the total number of individual variants thrown by *Lamarckiana* is much smaller than those *at present* thrown by *neo-Lamarckiana.* However, as has been noted, the seed sterility of *Lamarckiana* is very much higher than that of *neo-Lamarckiana* in the F_4 generation, and it is my working hypothesis that this fact is at least partly responsible for the smaller numbers of variants produced by the former.

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[5] Davis, B. M., "The Test of a Pure Species of *Œnothera,*" *Proc. Amer. Phil. Soc.,* LIV, 226–245, 1915.

Œnothera Lamarckiana of De Vries's cultures seems to me best interpreted as an impure species producing regularly because of its heterozygous or hybrid nature a number of classes of gametes relatively few of which, because of the extensive sterility, both gametic and zygotic, are able to form viable seeds different from those that reproduce the species. *Œnothera Lamarckiana* breeds true in its high degree because only the gametic combinations that reproduce *Lamarckiana* survive the mortality visited on most of the gametes and zygotes. By this view *Lamarckiana* is very much the reverse of a representative pure species which De Vries has assumed it to be and its "mutating habit" is the result of its hybrid origin and heterozygous nature rather than a spontaneous expression of homozygous germ plasm. The fact that the same types of "mutants" from *Lamarckiana* are produced by successive generations in fairly stable proportions indicates that their differentiation lies in the mechanism of segregation in heterozygous germ plasm rather than in a sporting tendency (mutation) which would be expected to express itself in ever-varying ways and degrees.

It is worth noting how different is the conception, here expressed, of the constitution of a pure species from the view formerly and probably now very generally held. Formerly a species was considered pure if it bred true. Now we believe that a species may be impure and still breed very largely or even wholly true if a degree of sterility is present sufficient to render abortive or infertile all types of gametes or zygotes that may be produced except the ones which carry forward the heterozygous line. The test of a pure species is then not that it should breed true (that is a corollary), but that it should produce gametes uniform except as they may differ with respect to the factors for sex characters.

In laying such great stress on the phenomena of gametic and zygotic sterility so very extensively present in the genus *Œnothera* it must not be supposed that we have as yet established the degrees to which sterility may be genetic in its character or to what extent it may be of a physiological nature. Only the sterility that has as its cause the failure of the reduction divisions to produce fertile gametes or the failure of the gametes to conjugate freely can properly be of a genetic nature. There is probably also a type of sterility due to physiological causes, as perhaps malnutrition, and this might affect gametes and zygotes which under favorable conditions would be fertile. We are very far from an understanding of the causes of sterility in *Œnothera,* to what extent cytological or to what degree physiological, and it would at present be most unsafe to carry lines of speculation very far in this field as regards the material under consideration.

Professor De Vries has expressed strongly a belief in the futility of my attempts to synthesize a *Lamarckiana*-like hybrid, taking the stand that unless the parent stock is known to be stable mutability might be inherited from one or both of the parent species, or that variants, the result of a cross from impure stock, might be mistaken for mutations. As a matter of fact *Œnothera biennis* is known to be unstable, producing a small series of "mutants," while *O. franciscana* has not been tested for its purity. Apparently Professor De Vries and I are working from assumptions that are far apart. The inheritance of a mutating habit such as that claimed for *Lamarckiana* would mean to me the inheriting of a heterozygous germ plasm running back to some hybrid origin. To me phenomena such as is exhibited by *Lamarckiana* in throwing its "mutants" indicates in itself the probability of heterozygous germ plasm. If this behavior is to be presented as evidence of mutation the purity of *Lamarckiana* must be established beyond all reasonable doubt and this in my opinion has not been shown. The tests of cross breeding, when twin hybrids result, and the very high degrees of gametic and zygotic sterility strongly indicate genetic impurity. And back of this is an obscure history for the material with no evidence it seems to me that *Lamarckiana* was ever present as a native species of any flora. The chief value which the study of my *Lamarckiana*-like hybrid may have for the problem of the origin and status of *Œnothera Lamarckiana* is likely to be a clearer understanding of how an obviously impure species, *neo-Lamarckiana,* may arise, a species which seems likely to present a breeding behavior parallel to that of *Lamarckiana,* and most important of all the significance of sterility in the working out of these results. It appears to me a matter of no vital importance to the status of a hybrid whether its parents are pure or impure. If markedly impure the problem of analysis for future generations merely becomes the greater. Since no species of *Œnothera* has as yet passed the tests for a pure species, we are at present in all of the *Œnothera* work talking of an abstraction when this concept is considered.

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August, 1916

STATISTICAL STUDIES OF THE NUMBER OF NIPPLES IN THE MAMMALS

It is perhaps not unnatural that a subject of such fundamental interest as that of the nourishment of the young in the mammals should have attracted the attention of observers from the time of the Greek philosophers. It is only within the last few years that attempts have been made to solve various problems by the application of the statistical method to series of quantitatively recorded data.

The materials may be divided for convenience of review.

Type, Variation and Correlation in Number of Mammæ

The statement made by Parker and Bullard,[1] on the basis of their splendid series of data for swine, that the standard deviation of the number of nipples is 0.6906 in the males and 0.7905 in the females at once arouses the suspicion of a biometrician. The constants actually are:

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[1] Parker, G. H., and C. Bullard, "On the Size of Litters and the Number of Nipples in Swine," *Proc. Amer. Acad. Arts and Sci.*, 49: 399–426, 1913.